TERRITORY ESTABLISHMENT, SIZE, AND TENACITY BY MALE RED-WINGED BLACKBIRDS

JAROSLAV PICMAN

Department of Biology, University of Ottawa, 30 Somerset E., Ottawa, Ontario K1N 6N5, Canada

ABSTRACT.—Most male Red-winged Blackbirds (*Agelaius phoeniceus*) established their first territories by replacing territory holders that disappeared. These territories were significantly larger than those established either through subdivision of the vacated territory between two or three replacement males, or through insertion of a new territory through displacement of one or more resident males. Almost all returning male Red-wings settled on their former territories in consecutive years. Their territories remained similar in size and location between years. Strong territory tenacity apparently is favored by lower costs of territory defense because of reduced aggression between familiar neighbors and site dominance effects. The lower costs of territory defense presumably also allowed the site-tenacious males to establish larger territories in consecutive years. Strong territory tenacity by returning males could explain much of the settlement pattern of new males. As a result, the spatial arrangement of male territories in the study marsh (i.e. the location of territorial boundaries) was similar in consecutive years. Traditionalism in the male territorial system should influence Red-wing mating patterns. *Received 27 January 1986, accepted 5 January 1987.*

MANY birds return to the same territories in consecutive years and frequently breed with previous mates (e.g. Richdale 1957; Coulson and White 1958, 1960; Krebs 1971; Richdale and Warham 1973; Picman 1981; Bédard and La-Pointe 1984; Cuthbert 1985; Gratto et al. 1985). Territory tenacity and mate fidelity may increase the fitness of returning individuals through accelerated pair formation (Lehrman and Wortis 1967, Morris and Ericson 1971, Ericson 1973), increased foraging efficiency, and improved escape from predators (e.g. Hinde 1956, Tinbergen 1957). Hence, site tenacity and mate fidelity play an important role in avian reproductive strategies.

Territory tenacity could affect significantly the mating pattern of polygynous species such as the Red-winged Blackbird (*Agelaius phoeniceus*; Searcy 1979, Picman 1981). Female Red-wings return to their previous territories in consecutive years, regardless of whether their previous mate returned (Picman 1981). As a result, new males may "inherit" the harems of the previous territory holders (Picman 1981). Previous studies on Red-wings suggest that males also generally return to their territories in subsequent years (Nero 1956, Case and Hewitt 1963, Searcy 1979). Because overwinter return rates of male Red-wings are relatively high (over 50%; Fankhauser 1967, Picman unpubl. data), the distribution of Red-wing territories should be similar

between years. This, along with strong female site tenacity, could lead to a high degree of "traditionalism" in both the distribution and number of male territories, and the distribution of females in a given marsh.

Territory tenacity should also be favored because of strong intrasexual competition for limited breeding space (Rohwer 1982). This is because familiarity reduces the level of aggression between neighbors (Yasukawa et al. 1982) and, thus, presumably lowers the costs of territory establishment by returning males. Strong site tenacity by returning males could, in turn, determine the location and size of territories established by new males. In addition, territory tenacity by returning males could influence the size of their territories. With respect to benefits associated with territory tenacity, the less tenacious individuals should experience higher rates of territorial interactions, and these could negatively influence the size of their territories. The lower costs of territory defense derived from the high degree of territory tenacity in returning males, however, should allow an increase in territory size in consecutive years if neighboring territories are vacated. Because breeding space is often limited in marsh-nesting Red-wings (e.g. Orians 1961, Hurly and Robertson 1985), acquiring a larger territory may increase the probability of acquiring a larger harem (Picman 1980b).

Returning to the same territory should be disadvantageous for males that experienced low reproductive success. To evaluate the role of previous breeding experience, we need to determine if territory size, harem size, and fledging success of males affect territorial shifts between years. This information should indicate the relative importance of intrasexual competition in determining the pattern of territory establishment by male Red-wings. Thus, if low reproductive success did not influence the degree of territory shifts, competition among males for breeding space presumably played the major role in favoring the high degree of territory tenacity by males.

I report the results of a 5-yr study on male Red-winged Blackbird territoriality. My objectives were to examine the pattern of territory establishment by new males; the degree of territory tenacity in males that returned to the marsh in consecutive years; the effect of territory size, mating success, and reproductive success on shifts of male territories between years; and the effect of territory tenacity on the size of male territories.

METHODS

The study was conducted between 1976 and 1980 in an extensive, brackish-water marsh at George C. Reifel Migratory Bird Sanctuary, on Westham Island, Delta, British Columbia. The higher grounds of this marsh are covered by a relatively homogeneous cattail (*Typha latifolia*) vegetation. Sedges (*Carex* sp.) and bulrushes (*Scirpus* sp.) dominate the lower areas near the seashore. Only two passerine species, the Red-winged Blackbird and the Marsh Wren (*Cistothorus palustris*), commonly breed in this marsh.

Early in April 1976 I established a grid system by dividing the study area (between 15 and 25 ha in different years) into 20 × 20-m quadrats. This made it possible to map the location of singing perches of male Red-wings and to quantify their interactions with intruders. Each year unbanded males were captured using a decoy trap (Picman 1979) and color-banded. Territories of individual males were determined each year in April and early May by recording the location of singing perches, flight paths, and interactions with conspecific intruders on maps of the study area. Territory sizes were calculated by the minimum convex polygon method.

Territory establishment by new males (i.e. males that appeared in the marsh for the first time) was studied by examining their recruitment into the breeding population. The effect of replacement of males that disappeared by single males on the loca-

tion of new territories, and the degree of territory tenacity by returning males, were examined in two ways. I measured the absolute overlap (m²) between the territories of a given male in successive years and the year-to-year change in size of the territories of returning males. To obtain an index of change in territory location, I divided the overlapping area of the new and previous territories by the size of the new territory. This index estimated the proportion of a new territory located within the previous territory of a given male, and ranged from 0 for a nonoverlapping territory to 1 for a new territory located within the previous territory. An index of change in territory size was estimated as follows: territory size in year 2 − territory size in year 1 + 6,500 (this constant was added to transform negative into positive values, and corresponds to the highest negative value of territory change due to territory size reduction from year 1 to 2). An Apple Graphics Tablet was used to analyze spatial data on territory size and the amount of overlap between new and previous territories of returning and replacement males. Methods of studying reproductive and mating success of males are described elsewhere (Picman 1980a, 1981). The critical level for rejecting a null hypothesis was $P < 0.05$. One-tailed tests were used whenever directional predictions could be made.

RESULTS

Pattern of territory establishment by new males. — A total of 95 territories defended by 61 males (3 present for 4 yr and 1 throughout the 5-yr study period) was observed. In 1977–1980, 41 new males established first territories in the study area (Table 1). Most new males (66%) replaced territory holders that disappeared from the study marsh ($n = 26$) or that abandoned their old territory and established a new territory elsewhere in the marsh ($n = 1$). Approximately 78% of territories established by replacement overlapped by at least 60% with the original territories (Fig. 1). Some replacement males expanded the territories of their predecessors by including areas located outside the breeding area in a previous year. This reduced the degree of overlap between the original and new territories. Despite these changes, the original and new territories were similar in size (Table 2). As a result, the size of new territories established by replacement males correlated significantly with the original territory size ($r = 0.60$, df = 17, $P < 0.001$).

Eight adult males established their first territories by dividing three vacated territories between 2 ($n = 1$) or 3 ($n = 2$) replacement indi-

TABLE 1. Recruitment of male Red-winged Blackbirds into the breeding population, 1977–1980.

| | Number of new males settling in: | | | | |
Mode of territory establishment	1977	1978	1979	1980	1977–1980
Replacement of a male that disappeared	8	8	3	8	27
Division of vacated territory between 2–3 new males	—	—	8	—	8
Insertion through displacement of 1–3 males from part of their territories	1	—	4	1	6
Total no. of new males	9	8	15	9	41

viduals. Six of these males settled on two adjacent territories that were vacated in the same year (Fig. 2). The division of a territory between two or three new individuals was associated with significantly larger original territories as compared with territories of predecessors of the replacement males (U-test, P < 0.05; Table 2). The division reduced the territory sizes for the new males compared with territories established through one-to-one replacement (U-test, P < 0.05; Table 2). All cases of territory establishment through division occurred in 1979 (Table 1), when male density was slightly higher (Table 3). Thus, more males may have competed for breeding space in 1979. This intense competition produced more frequent divisions of territories between new males. This suggestion was supported indirectly by the fact that in 1977 and 1978 there were 5 large vacated territories (12,892–16,932 m²; mean = 14,989 m²), all claimed by individual replacement males. In contrast, in 1979 all vacated territories over 11,000 m² (n = 3) were divided among several males (the difference between 1977–1978 and 1979 was statistically significant; Fisher exact test, P = 0.018). I suggest that the presence of large territories and intense male-male competition are both important determinants of division as a mode of territory establishment by new males.

Six new males (2 yearlings, 4 adults) gained access to breeding space by displacing 1–3 res-

ident males from parts of their territories. Territories established through insertion were significantly smaller than those established by replacement (U-test, P < 0.01; Table 2) but did not differ significantly from territories established through division (U-test, P > 0.05; Table 2). This mode of territory establishment was uncommon and may have occurred because the inserted territories were in suboptimal habitats (mostly outside the normal breeding habitat) that always attracted few females (Picman unpubl. data), or because territories of the displaced males were large (11,898 and 15,340 m²) and presumably more difficult to defend (see Fig. 5). In one case a returning male established a territory mostly outside his original one, and this might have enabled a new male to insert a new territory. Four of the 6 cases of territory insertion occurred in 1979 (Table 1), possibly because competition among males for limited breeding space was stronger in that year.

In 5 cases the disappearance of the original male led to division of the vacated territory among the neighboring resident males. Unlike the cases of new males that established their territories through replacement or division (see Table 2), this loss of territories involved originally small territories (Table 2; size difference between these two types of territories was significant statistically; U-test, P < 0.025).

Most new males established territories

TABLE 2. Territory size established by new males through replacement, division, or insertion related to the territory size of previous occupants. Territories divided between neighbors following the disappearance of the resident male averaged 4,811 m² (±2,801, n = 5).

| | Mean size (m²) ± SD of territories of: | | | | |
| | Previous males | n | New males | n | P[a] |
Territory history					
Vacated territory defended by a replacement male	8,934 ± 3,573	27	8,866 ± 3,201	27	>0.8
Vacated territory divided between 2–3 new males	15,267 ± 3,584	3	5,857 ± 2,638	8	<0.05
New territory inserted between existing territories	—	—	5,171 ± 2,097	6	—

[a] Sizes of new and previous territories were compared by Mann-Whitney U-tests.
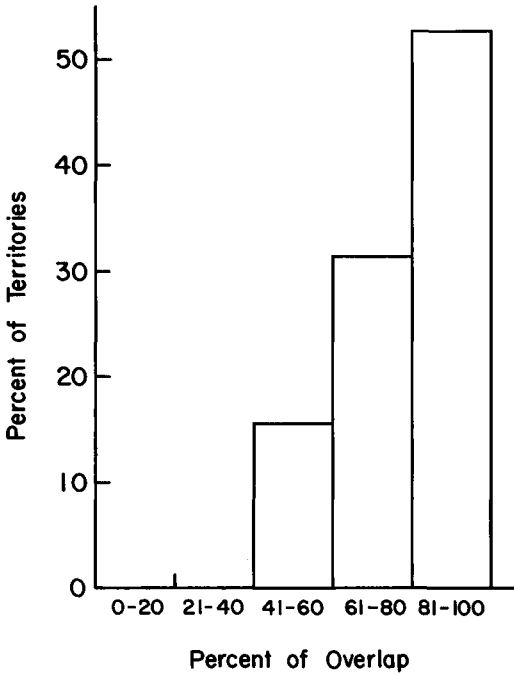
Fig. 1. Percentage of overlap between territories established by replacement males and those defended by previous territory holders.

TABLE 3. Size of male Red-winged Blackbird territories, 1976-1979.[a]

Year	Mean territory size (m²) ± SD	Range (m²)	n
1976	8,891 ± 4,118	3,122–16,932	15
1977	8,548 ± 4,293	1,188–16,196	18
1978	9,923 ± 3,815	3,619–18,456	18
1979	7,188 ± 2,512	2,196–12,293	25
1980	7,618 ± 2,566	3,713–13,652	19

[a] Territories did not differ significantly among years; 1-way ANOVA, $F(4,90) = 2.41$, $P > 0.1$.

ment by new males resulted in the maintenance of the quantity and location of previous territories. Insertion of new territories and division of original territories added new territories, whereas division of vacated territories between neighboring males resulted in the loss of territories.

Territory tenacity by resident males.—Of the 61 males recorded, 23 returned at least once (the total number of return years by all males was 34). In only 2 of the 34 cases a male abandoned his original territory and established a new one (in one case adjacent to the previous territory; the second case involved a male that established a new territory as an adult approximately 600 m from the territory he held as a yearling). Thus, most (94%) males returned to their former territories in the subsequent year.

through replacement. This mode of territory establishment also produced the largest average territories for new males (Table 2). Division of previous territories was less common and resulted in smaller territories that generally were located in high-quality breeding areas. Insertion of new males seems least advantageous because of the smaller and sometimes less suitable breeding space acquired. One-to-one replace-
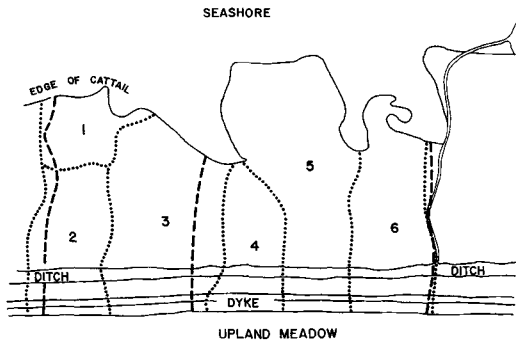

Fig. 2. Example of division of two vacated territories (boundaries shown by dashed lines) among 6 new males in 1979 (dotted lines).
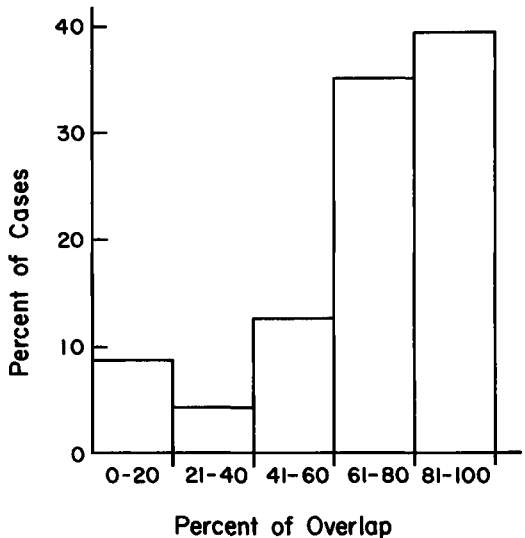

Fig. 3. Overlap between territories defended by male Red-wings returning in consecutive years (one-year comparisons).
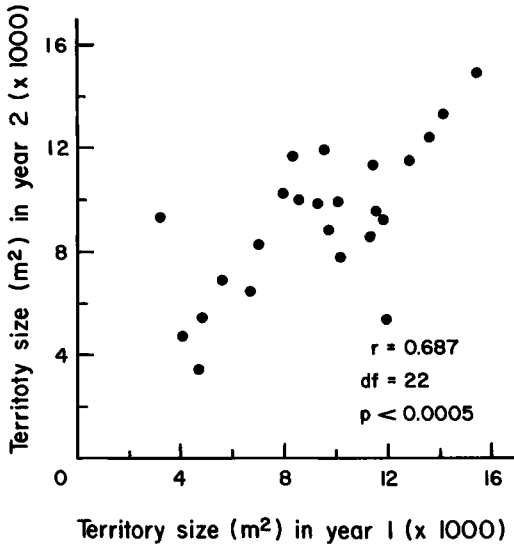
Fig. 4. Effect of site tenacity on size of territories of male Red-wings returning in consecutive years. Data from years 1–2, 2–3, 3–4, and 4–5 were combined.

TABLE 4. Proportion of overlap between previous and new territories of males present for 2–5 consecutive years. The proportion of overlap was defined as the overlapping area between new and previous territories divided by the size of the new territory.

Comparison	Mean proportion of overlap $\pm$ SD	n
One-year[a]	0.78 ± 0.18	31
Two-year[b]	0.70 ± 0.31	8
Three-year[c]	0.50 ± 0.13	3
Four-year	0.45	1

[a] Data on territories from years 1–2, 2–3, 3–4, and 4–5 were combined.
[b] Data from years 1–3, 2–4, and 3–5 were combined.
[c] Data from years 1–4 and 2–5 were combined.

The index of overlap (see Methods) indicated that in one-year comparisons most males exhibited high territory tenacity (Table 4). For 79% of returning males the overlap between new and previous territories was at least 61% (Fig. 3), with a mean overlap of 78% (Table 4). As a result, the size of territories defended by the same individuals in consecutive years was correlated significantly (Fig. 4). In two-year, three-year, and four-year comparisons the degree of overlap between previous and new territories of returning males decreased gradually (Table 4). The degree of territory tenacity was likely to be underestimated, however, because of changes in vegetation structure between years that may have caused expansion or contraction of some peripheral territories. The majority of male Red-wings that returned in consecutive years exhibited strong site tenacity, which resulted in the maintenance of similar boundaries.

I examined the effects of territory tenacity exhibited by returning males and recruitment of new males through replacement on the spatial organization of Red-wing territories by comparing the index of overlap between original and new territories. The index of overlap for the returning males for one-year comparisons [0.78 ± 0.18 (SD), $n = 31$; Table 4] was similar to that for territories of previous and replacement males [0.76 ± 0.18 (SD), $n = 27$; the two were not significantly different: $t = 0.3$, $P > 0.7$]. Thus, the tendency of males to return to their previous territories and the establishment of territories by new males through replacement contributed similarly to the stability of the spatial organization of Red-wing territories between years.

The effect of territory size, harem size, and reproductive success on shifts of male territories.—The greater territory shifts between consecutive years exhibited by some males (Fig. 3) might result from two processes. First, males that defend small territories should attempt to increase their chances of acquiring more females and hence of producing more offspring by subsequently establishing a larger territory. To test this hypothesis, I correlated the size of the previous territories with the index of change in size of territories defended by the same males in two consecutive years. A highly significant negative correlation between the size of previous territories and the index of change in territory size (Fig. 5) supports the hypothesis of increased size of small territories. Thus, males whose territories in year 1 were small defended larger territories in year 2. Individuals that defended large territories in year 1, however, established smaller territories in year 2 (Fig. 5). These results were also consistent with an alternative hypothesis that territory size varied randomly from year to year. The hypothesis predicts that when there is a fixed range of territory sizes, small territories are likely to become larger and vice versa. Both hypotheses make the same prediction about changes in size of small and large territories and are, thus, difficult to discriminate.
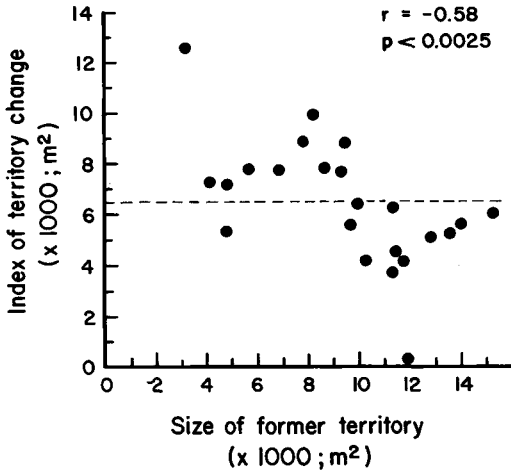
r = -0.58
p < 0.0025

Fig. 5. Relationship between territory size in year 1 and the index of change in size of territories defended by returning male Red-wings in years 1 and 2. The dashed line indicates no change in territory size in two consecutive years; territories increased and decreased relative to year 1 above and below this line, respectively.

In the second process greater territory shifts between years should follow low mating or reproductive success. To test this hypothesis, I correlated the index of overlap between the new (year 2) and previous (year 1) territories of returning males with the total number of young raised on a given territory, average number of young fledged per female, and harem size in year 1. The change in location of territories of individual males between years did not correlate significantly with any of these factors (Table 5). Therefore, I reject the hypothesis that poor reproductive success or small harems promoted greater territory shifts between years.

The effect of territory tenacity on territory size.— To test the hypothesis that tenacity allows defense of larger territories, I correlated the index of overlap between subsequent territories of returning males with the change in size of their new relative to their previous territory. Because the amount of overlap should, in this case, be related to the previous territory, the index of overlap used in this analysis was calculated as the overlapping area divided by the size of the previous territory. Results of this analysis indicated a positive, statistically significant trend between the degree of territory tenacity and the amount of change in the size of new, relative to previous, territories ($r = 0.39$, df $= 31$, $P <$

TABLE 5. Simple correlations between the index of change in territory location (the area of overlap of previous and new territories divided by the size of the new territory) (A) and the total number of young fledged per male (B), the number of young fledged per female (C), and the harem size in year 1 (D).

Correlation	Correlation coefficient	df	P (1-tail)
A with B	0.116	31	>0.25
A with C	-0.174	31	>0.1
A with D	0.272	31	>0.05

0.025). Thus, strong territory tenacity on average increased the male's chances of acquiring a larger territory in subsequent years.

DISCUSSION

Recruitment of new males into the breeding population resembled that described for new males by Nero (1956). My data suggest that establishment of first territories through one-to-one replacement on average produced larger territories. Breeding space probably is limited in marshes for Red-winged Blackbirds of both sexes (e.g. Orians 1961, Hurly and Robertson 1985). Thus, establishing larger territories should increase a male's chance of acquiring a larger harem. This hypothesis is supported by a positive correlation between territory size and harem size in the population (Picman 1980b, in prep.). Hence, individuals that establish larger territories are favored. The finding that replacement of territory owners by single males is the most common mode of establishment of territories by new male Red-wings is consistent with this proposition.

Most male Red-wings returned to their previous territories in consecutive years. This has been observed in other Red-wing populations (Nero 1956, Case and Hewitt 1963, Searcy 1979), and strong territory tenacity is probably characteristic of this species. My results suggest further that the tendency of males to return to the same territory continues throughout their reproductive life, in spite of the fact that some individuals always attracted few females or raised only a small number of young. There are, however, great differences in territory quality in this marsh (Picman 1980b), and at least some features that determine territory quality affect fitness directly (e.g. the abundance of Marsh

Wrens; Picman 1980a). Hence, some males should attempt to move to better habitats where their reproductive success would be higher. But Red-wings did not behave in this way.

Searcy (1979) and Oring (1982) suggested that strong territory tenacity could result from the following four situations. First, males return to their previous territories because vacant areas are of lower quality. Second, males cannot assess habitat quality effectively. Third, territory tenacity increases fitness because of familiarity with the location of foraging grounds and sites safe from predators. And fourth, site dominance or prior residency effects should make it easier for males to reclaim their former territory (Rohwer 1982).

The first three situations are less important to the Reifel Sanctuary marsh population because some vacant areas attracted many females or produced relatively many young in the previous year; nest predation rates could be predicted from the presence of Marsh Wrens, which settle before Red-wings; the impact of Marsh Wrens is reduced through female clumping; and most foraging occurs off territories (Picman 1980a, b). The fourth hypothesis provides the most plausible explanation for the following reasons. Resident male Red-wings are more tolerant of familiar neighbors than of strange intruders, presumably as a result of associative learning (Yasukawa et al. 1982). This may explain why newly settling males interact more aggressively with their neighbors than returning males do with familiar neighbors (Nero 1956). Hence, male Red-wings should return to their previous territories in consecutive years to reduce the costs of territory establishment and maintenance. This view is consistent with evidence that males with some experience in a given area before attempted establishment of their first territory are more successful in establishing themselves in that area than individuals without previous experience (Yasukawa 1979).

In addition to reduced costs of territory defense, site dominance should accelerate territory establishment. Competition among male Red-wings for breeding space is strong, as indicated by removal experiments (Orians 1961), high trespass rates by intruding males (Peek 1971), and defense of suboptimal areas (e.g. Robertson 1972, 1973). Therefore, rapid territory establishment by males should be impor-

tant. The reduced costs of territory defense may allow territory expansion when some of the adjacent territories are vacated (the overwinter survival of males is about 50%). Accordingly, males that returned to their territories increased their territories more than males whose territories shifted between years.

The settlement pattern of new individuals recruited into the breeding population could be explained largely by strong male territory tenacity. Because older males return to their former territories, new individuals usually can settle only on the vacated territories. Hence, strong competition for breeding space promotes territory tenacity in returning males, and the benefits associated with establishing a larger territory (i.e. more females) explain why most new males established their first territories through one-to-one replacement. At present, however, it is not known whether the pattern of settlement of new males on vacated territories of various quality is random or if it is determined by differences in the males' competitive ability.

Strong territory tenacity in males promotes stability in the Red-wing territorial system. Changes in territory number, location, and size are likely to be introduced by division of vacated territories among neighbors, division of originally large territories among several replacement males, insertion of new territories between existing ones, and simultaneous disappearance of several neighbors. These events, in turn, appear to be determined by the size of the vacated territories (Table 2), the overwinter mortality pattern of the resident males, and probably the number of new males competing for the vacated areas. These events were relatively infrequent in the Reifel Sanctuary marsh (Table 1), and were responsible for only relatively minor disruptions of the "traditional" nature of the Red-wing territorial system.

Strong site tenacity has important consequences for the Red-wing polygynous mating pattern. Because most female Red-wings also return to the same area in consecutive years (Picman 1981), the mating success of new males is influenced by the number of females that bred in their territories in the previous year (Picman 1981). Territory tenacity exhibited by males and females thus plays an important role in determining the mating pattern in Red-wing populations.

Literature Cited

Bédard, J., & G. LaPointe. 1984. The Savannah Sparrow territorial system: can habitat features be related to breeding success? Can. J. Zool. 62: 1819–1828.

Case, N. A., & O. H. Hewitt. 1963. Nesting and productivity of the Red-winged Blackbird in relation to habitat. Living Bird, Ann. Cornell Lab. Ornithol. 2: 7–20.

Coulson, J. C., & E. White. 1958. The effect of age on the breeding biology of the Kittiwake (Rissa tridactyla). Ibis 100: 40–51.

———, & ———. 1960. The effects of age and density of breeding birds on the time of breeding of the Kittiwake, Rissa tridactyla. Ibis 102: 71–86.

Cuthbert, F. J. 1985. Mate retention in Caspian Terns. Condor 87: 74–78.

Ericson, C. J. 1973. Mate familiarity and the reproductive behavior of Ringed Turtle Doves. Auk 90: 780–795.

Fankhauser, D. P. 1967. Survival rates in Red-winged Blackbirds. Bird-Banding 38: 139–142.

Gratto, C. L., R. I. G. Morrison, & F. Cooke. 1985. Philopatry, site tenacity, and mate fidelity in the Semipalmated Sandpiper. Auk 102: 16–24.

Hinde, R. A. 1956. The biological significance of the territories of birds. Ibis 98: 340–369.

Hurly, T. A., & R. J. Robertson. 1985. Do female Red-winged Blackbirds limit harem size? I. A removal experiment. Auk 102: 205–209.

Krebs, J. R. 1971. Territory and breeding density in the Great Tit, Parus major L. Ecology 52: 2–22.

Lehrman, D. S., & R. P. Wortis. 1967. Breeding experience and breeding efficiency in the Ring Dove. Anim. Behav. 15: 223–228.

Morris, R. L., & C. J. Ericson. 1971. Pair bond maintenance in the Ring Dove (Streptopelia risoria). Anim. Behav. 19: 398–406.

Nero, R. W. 1956. A behavior study of the Red-winged Blackbird. II. Territoriality. Wilson Bull. 68: 129–150.

Orians, G. H. 1961. The ecology of blackbird (Agelaius) social system. Ecol. Monogr. 31: 285–312.

Oring, L. W. 1982. Avian mating systems. Pp. 1–92 in Avian biology, vol. 6 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

Peek, F. W. 1971. Seasonal change in the breeding behavior of the male Red-winged Blackbird. Wilson Bull. 83: 383–395.

Picman, J. 1979. A new technique for trapping female Red-winged Blackbirds. North Amer. Bird Bander 4: 56–57.

———. 1980a. Impact of Marsh Wrens on reproductive strategy of Red-winged Blackbirds. Can. J. Zool. 58: 337–350.

———. 1980b. Behavioral interactions between Red-winged Blackbirds and Long-billed Marsh Wrens and their role in the evolution of the Redwing polygynous mating system. Ph.D. dissertation, Vancouver, Univ. British Columbia.

———. 1981. The adaptive value of polygyny in marsh-nesting Red-winged Blackbirds; renesting, territory tenacity, and mate fidelity of females. Can. J. Zool. 59: 2284–2296.

Richdale, L. E. 1957. A population study of penguins. Oxford, Clarendon Press.

———, & J. Warham. 1973. Survival, pair bond retention and nest site tenacity in Buller's Mollymawk. Ibis 115: 257–263.

Robertson, R. J. 1972. Optimal niche space of the Red-winged Blackbird (Agelaius phoeniceus). I. Nesting success in marsh and upland habitat. Can. J. Zool. 50: 247–263.

———. 1973. Optimal niche space of the Red-winged Blackbird: spatial and temporal patterns of nesting activity and success. Ecology 54: 1085–1093.

Rohwer, S. 1982. The evolution of reliable and unreliable badges of fighting ability. Amer. Zool. 22: 531–546.

Searcy, W. A. 1979. Male characteristics and pairing success in Red-winged Blackbirds. Auk 96: 353–363.

Tinbergen, N. 1957. The functions of territory. Bird Study 4: 14–27.

Yasukawa, K. 1979. Territory establishment in Red-winged Blackbirds: importance of aggressive behavior and experience. Condor 81: 258–264.

———, E. I. Bick, D. W. Wagman, & P. Marler. 1982. Playback and speaker-replacement experiments on song-based neighbor, stranger, and self discrimination in male Red-winged Blackbirds. Behav. Ecol. Sociobiol. 10: 211–215.